Thelodont, Acanthodian, and Chondrichthyan Fossils from the Lower Devonian of southwest China

WANG NIANZHONG (WANG NIEN-CHUNG)
(Communicated by A. RITCHIE)

WANG NIANZHONG. Thelodont, acanthodian, and chondrichthyan fossils from the Lower Devonian of southwest China. *Proc. Linn. Soc. N.S.W.* 107 (3), (1983) 1984: 419-441.

Thelodont, acanthodian, and chondrichthyan remains have been extracted from bone beds in the Xitun Member of the Cuifengshan Formation (Lower Devonian) in south China by treatment with acetic acid. The thelodontid *Turinia asiatica* sp. nov., and the chondrichthyans *Gualepis elegans* gen. et sp. nov., *Changolepis tricuspidus* gen. et sp. nov., *Peilepis solida* gen. et sp. nov., and *Ohiolepis ? xitunensis* sp. nov., are the first records of these groups in the Devonian of China. The acanthodians *Youngacanthus gracilis* gen. et sp. nov., Ischnacanthidae gen. indet., and *Nostolepis* sp. indet. are the first reliable reports of Devonian acanthodians from Yunnan. It is concluded that the South China block may have been closer to Baltica and North America in the Early Devonian than to the other main tectonic blocks. There may have been some primitive thelodontids before the mid-Silurian in China, from which *Hanyangaspis* Pan *et al.* (Agnatha) and some advanced thelodontids developed. The mode of development of the cephalic shield in *Hanyangaspis* may be very similar to that of heterostracans, judging from the ornamentation of the cephalic shield in *Hanyangaspis* compared to the scale crowns of *Thelodus sculptilis* Gross and *T. admirabilis* Marss, and the ornamentation of the cephalic shield in *Porophoraspis* Ritchie and Tomlinson. There are two horizons containing acanthodians in south China — in the Lower Devonian deposits of southwest China, and in the Silurian deposits of the middle and lower reaches of the Yangtze River. Climatiid and ischnacanthid remains occur in both, but there are no genera in common. The presence of chondrichthyans suggests that the Xitun Member was marginal marine.

Wang Nianzhong, Institute of Vertebrate Palaeontology and Palaeoanthropology, Academia Sinica, P.O. Box 643, Beijing (28) China. *A paper read at the Symposium on the* Evolution and Biogeography of Early Vertebrates, *Sydney and Canberra, February 1983; accepted for publication 18 April 1984, after critical review and revision.*

INTRODUCTION

Thelodont, acanthodian and elasmobranch vertebrate microfossils have not previously been recorded from the Early Devonian of China, and their apparent absence has attracted some comment (e.g. Blieck and Goujet, 1978; Young, 1981, 1982). It is of some interest therefore to be able to report here an abundant and diverse microvertebrate assemblage in the Xitun Member of the Cuifengshan Formation (Qujing district, Yunnan Province). At my disposal are numerous thelodont, acanthodian, and chondrichthyan scales of varying size and shape, a few fragments of acanthodian dentigerous jaw bones, and several isolated chondrichthyan teeth. All were extracted by treatment with dilute acetic acid from samples of greenish-grey argillaceous limestone or greenish-yellow siltstone from the Xitun Member. As well as thelodonts, acanthodians, and chondrichthyans, there are, in the same member, other microvertebrate fossils (Actinopterygii, Crossopterygii, Dipnoi, Placodermi, etc.). These will be dealt with elsewhere. Material described below is housed in the Institute of Vertebrate Palaeontology and Palaeoanthropology (IVPP), Beijing, China.

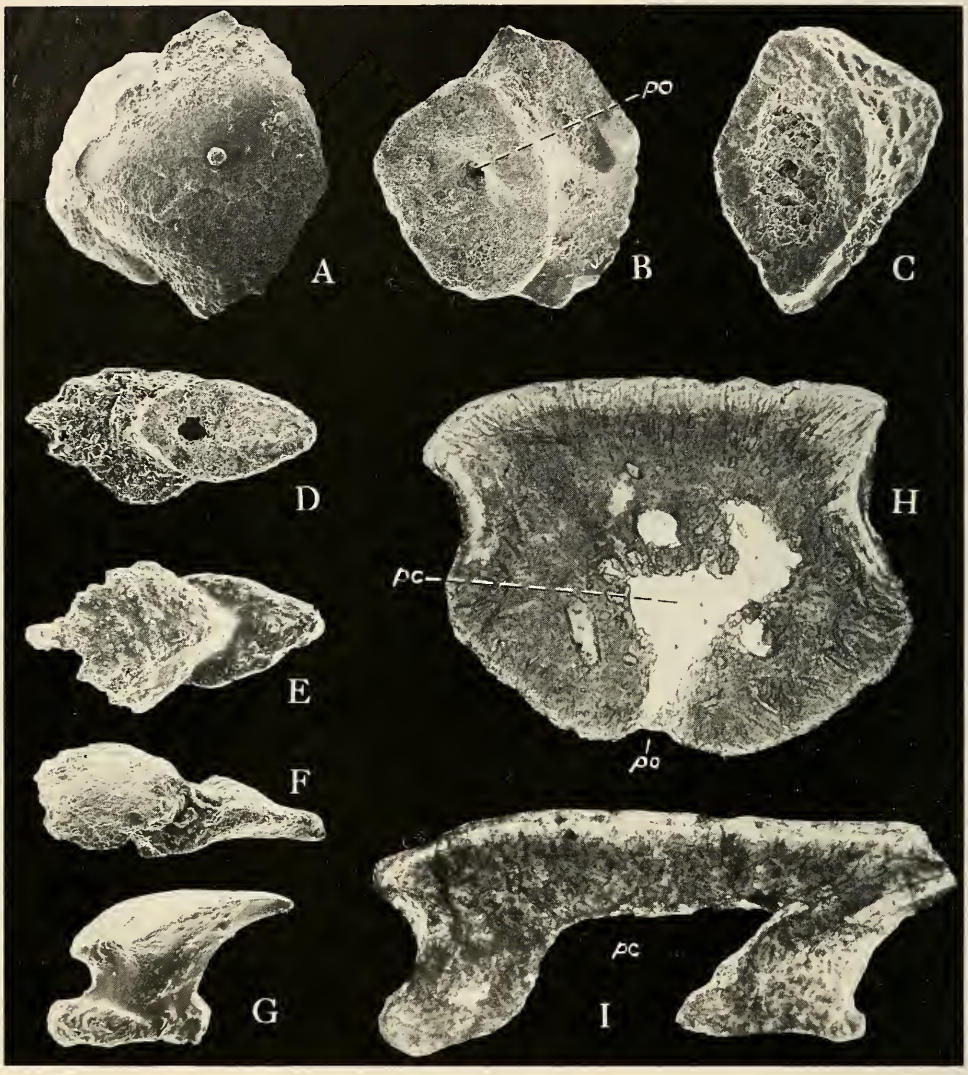


Fig. 1. Turinia asiatica sp. nov. V7215. **A** and **B**, No. 7 (× 75), head scale. **A**, crown view; **B**, basal view. **C**, No. 9 (× 105), basal view of a body scale. **D**, No. 2 (× 71), basal view of a body scale. **E**, No. 3 (× 71), crown view of a body scale. **F**, No. 4 (× 71), crown view of a body scale. **G**, No. 5 (× 71), lateral view of a transitional scale. **H**, No. 1 (× 113), vertical longitudinal section of a body scale. **I**, No. 8 (× 113), vertical longitudinal section of a body scale. *pc*, pulp cavity; *po*, pulp opening.

Systematic Description

Subclass THELODONTI
Order THELODONTIDA
Family TURINIIDAE Obruchev 1964
Genus *TURINIA* Traquair 1896
Turinia asiatica sp. nov.
Figs 1, 2

Diagnosis: Small head, transitional, and body scale types. Crowns rounded, elliptical,

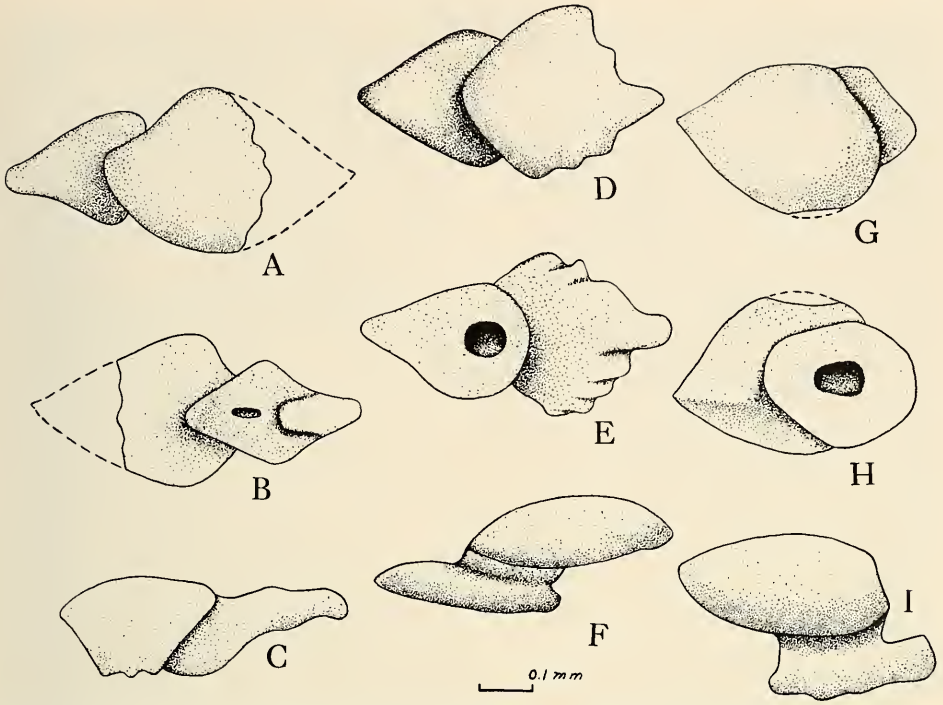


Fig. 2. Turinia asiatica sp. nov. V7215. **A-C**, crown, basal, and lateral views of No. 4: **D-F**, crown, basal, and lateral views of a body scale, No. 3; **G-I**, crown, basal and lateral views of a transitional scale, No. 5 (all × 70).

or rhombic, with a smooth unornamented surface and smooth or dentate posterolateral margins; wall of scale neck smooth; scale base rounded, elliptical, or irregular in shape, with a prominent anterior process; *Thelodus*-type histology (*sensu* Gross, 1967), with a large pulp cavity and a small central pulp opening; dentine tubules long and densely distributed.

Holotype: V7215.3, a body scale.

Other material. V7215.7, a head scale; V7215.5, a transitional scale, and V7215.2,4,9, three body scales; V7215.1, a longitudinal section of a head scale, and V7215.8, a longitudinal section of a body scale.

Locality and Horizon. Xitun member of the Cuifengshan Formation (Lower Devonian), Qujing district, East Yunnan, China.

Description: The small scales range in maximum rostrocaudal length from 0.30 to 0.60 mm (Table 1). They may be separated into head, transitional, and body scale types. The head scales have a rounded crown, with a simple smooth and unornamented crown surface. The wall of the scale neck is smooth and the base is rounded with a large pulp cavity of *Thelodus*-type (Gross, 1967; Moy-Thomas and Miles, 1971), and a small pulp opening. The transitional scales have an elliptical and slightly convex crown, with a small posterior cusp, and a shallow base with a middle-sized pulp opening. The body scales possess an elliptical or rhombic crown, with a smooth but slightly convex surface, a smooth anterolateral margin, and a smooth or dentate posterolateral edge. The wall of the neck is smooth, and the shallow base is the same depth in both anterior and posterior parts (e.g. specimens V7215.2 and 3). Commonly the base is elongated to

TABLE 1

Turinia asiatica *sp. nov. Dimensions of scales (in mm)*

V.7215	Length of crown	Breadth of crown	Length of base	Breadth of base	Depth of scale	Length of scale
2	0.04	0.28	0.35	0.18	0.20	0.53
3	0.37	0.30	0.32	0.20	0.20	0.60
4	0.35	0.30	0.30	0.20	0.20	0.60
5	0.37	0.30	0.28	0.20	0.30	0.50
7	0.50	0.50	0.30	0.35	0.35	0.55
9	0.27	0.32	0.17	0.30	0.15	0.30

form a prominent anterior process (e.g. specimen V7215.4). The base has a pulp opening of small or medium size in a posterior or central position. The dentine tubules are long and densely distributed.

Remarks: These scales resemble in some respects those of *Turinia polita* Kar.-Tal. from the Lower Devonian of Lithuania, Volynia, and Podolia, USSR (Karatajute-Talimaa, 1978), but they differ in their smaller size, in having fewer denticles at the posterolateral margin of the crown in the body scales, and in possessing more dentine tubules in the crown. There is also a resemblance, particularly in the more elongate scales, to those described by Hoppe (1931) as *Thelodus trilobatus.* This form ranges from the lower Ludlow to lower Downtonian in Europe (Turner, 1976), and may be close to the ancestry of the turiniids according to Karatajute-Talimaa (1978). With the new species described here generic assignment is uncertain, and for the present it is described as a new species of the genus *Turinia.*

Subclass ACANTHODII Owen 1846
Order CLIMATIIDA Berg 1940
Family CLIMATIIDAE Berg 1940
Genus *NOSTOLEPIS* Pander 1856
Nostolepis sp. indet.
Fig. 3

Material: V7216.1,4,5,7, and a section V7216.2, all body scales.
Locality and Horizon: As for V7215.
Description: Among the acanthodian scales of the Xitun member, one type, represented by V7216.1,4,5 and 7, comes mainly from the argillaceous limestone. These scales have more or less rhomboidal-shaped crowns which may be flat (e.g. 7) or elevated (e.g. 4). The ornamentation of the crown is of two types: a few long ridges extend from the anterior part of the crown to the posterior margin, converging posteriorly (Fig. 3**D-F**), or more and shorter ridges are restricted to the anterior part of the scale crown (Fig. 3**A-C**). The scale base is rhombic in shape, and clearly tumid. Its anterior margin may be more advanced than that of the crown (Fig. 3**D**), or it may extend forward as far as the anterior margin of the crown (Fig. 3**C**). The scale has a clear constricted neck between the crown and base. Scale dimensions are given in Table 2.

The structure of these scales is of the *Nostolepis*-type (Denison, 1979; Gross, 1940, 1947, 1957, 1971). There is a crown of mesodentine tissue which is penetrated by vascular canals, and a base of cellular bone (Fig. 3**G**).

Remarks: The material dealt with here is referable to the genus *Nostolepis* according to scale shape and structure, but it is not clear from the available material whether or not it represents a new species.

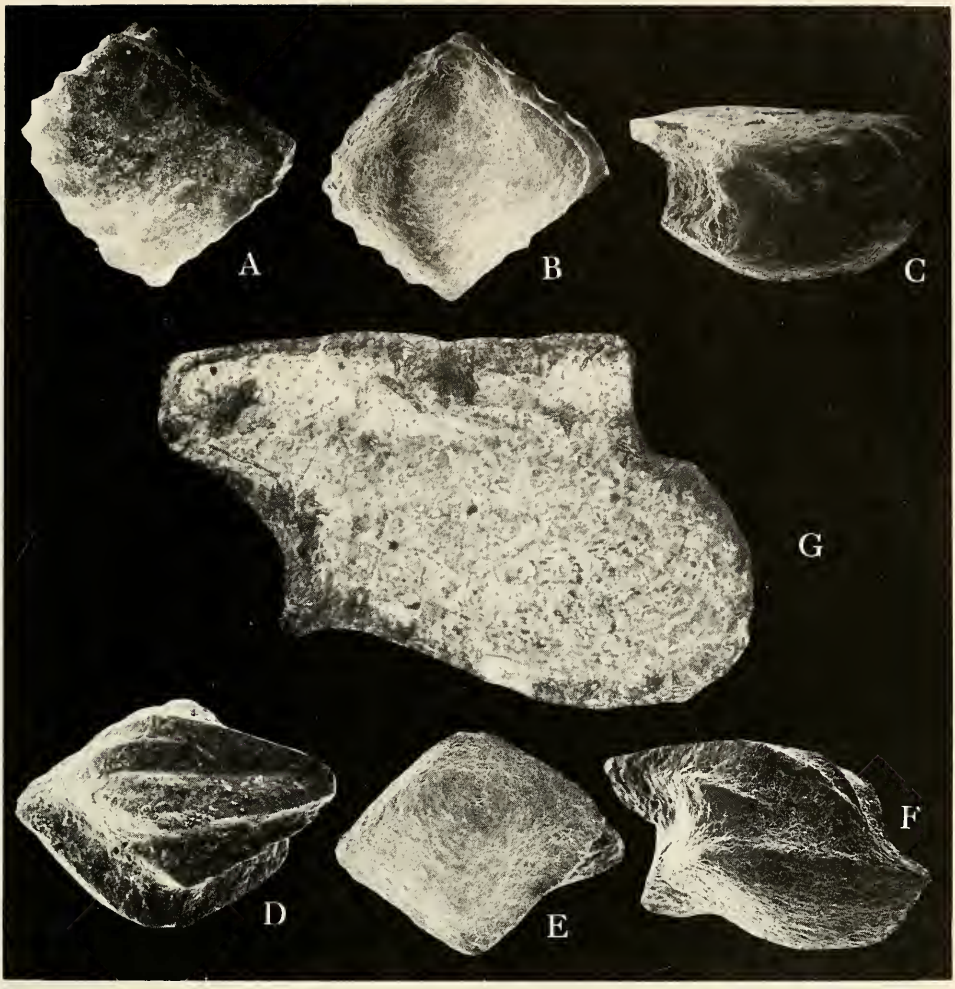


Fig. 3. Nostolepis sp. indet. V7216. **A-C**, isolated scale, No. 7. **A**, crown view; **B**, basal view, and **C**, slightly oblique lateral view (× 72). **D-F**, isolated scale, No. 4. **D**, crown view (× 96); **E**, basal view, (× 72), and **F**, lateral view (× 96). **G**, vertical longitudinal section of scale No. 2 (× 176).

Order ISCHNACANTHIDA Berg 1940
Family ISCHNACANTHIDAE Berg 1940
Genus *YOUNGACANTHUS* nov.

Diagnosis: Teeth anchylosed to the jaw bone; main tooth cusps of the dentigerous jaw bone stout, triangular in parabasal section, and with three dentine ridges at anterior, posterior, and medial margins of the main tooth cusp; each main tooth cusp having two small anterior side cusps and two small posterior side cusps, but medial side cusps are absent.

Youngacanthus gracilis sp. nov.
Figs 4,5

TABLE 2

Nostolepis *sp. indet. Dimensions of scales (in mm)*

V.7216	Length of crown	Breadth of crown	Length of base	Breadth of base	Depth of scale
7	0.65	0.60	0.60	0.60	0.30
4	0.50	0.30	0.45	0.40	0.20
1	0.60	0.50	0.50	0.60	0.30
5	0.80	0.60	0.70	0.70	0.70

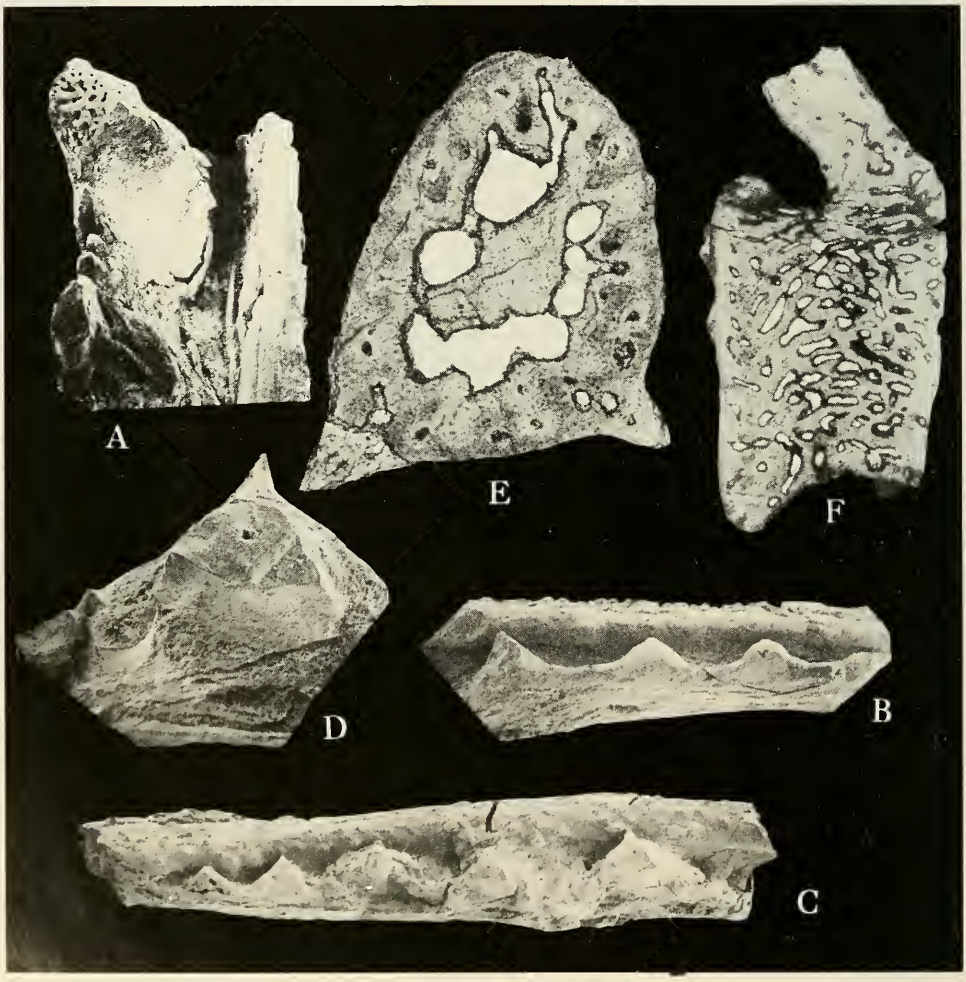


Fig. 4. Youngacanthus gracilis gen. et sp. nov. V7217. **A**, holotype, crown-medial view of part of a dentigerous jaw bone (× 14.4); **B**, crown-exterior view of part of a dentigerous jaw bone, No. 2 (× 17); **C**, crown view of part of a dentigerous jaw bone, No. 3, oriented with its anterior part to the right (× 16); **D**, detail of second main cusp in C (× 58); **E**, parabasal section of a main cusp, No. 4 (× 136); **F**, vertical transverse section of a dentigerous jaw bone, No. 5 (× 32).

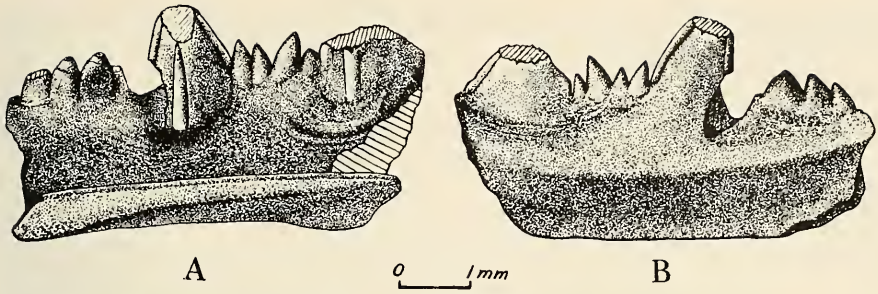


Fig. 5. Youngacanthus gracilis gen. et sp. nov. Holotype, V7217, in medial (**A**) and exterior views (**B**).

Derivation of name: After the late Professor C. C. Young, *akantha* (Gr.), a thorn, and *gracilis* (L.), slender.
Holotype: V7217.1, a fragment of dentigerous lower jaw bone.
Other material: V7217.2 and 3, two other fragments of dentigerous jaw bones; V7217.4, a parabasal section of an isolated tooth, and V7217.5, a vertical transverse section through the dentigerous jaw bone.
Locality and Horizon: As for V7215.
Diagnosis: As for genus (the only species).
Description: The dentigerous jaw bones are slender and h-shaped in transverse section. The dentigerous side is much higher than the medial side at the face of the crown. There are many tubercles on the surface of the medial side. The basal part of the jaw bone is concave upwards, perhaps a cavity for the meckelian cartilage. Numerous vascular spaces are observed in the transverse sections (Fig. 4**F**).

The teeth anchylosed to the jaw bone consist of large main tooth cusps and small anterior and posterior side-cusps. The jaw bone carries two main tooth cusps and six side tooth cusps in the holotype, five main cusps and twelve side cusps in specimen V7217.2, and four main cusps only in V7217.3. The main tooth cusps and side cusps vary in size and shape: they become smaller and show more wear towards the posterior end, so the characteristics of the main and side tooth cusps are clearer in the anterior part of the jaw bone than posteriorly.

Each cone-shaped main tooth cusp is triangular in parabasal section, and shows a pulp cavity divided into several small parts (V7217.4). It carries three triangular dentine ridges at its anterior, posterior, and medial sides. Only the ridges on the anterior and posterior sides extend upwards to the tip of the tooth. Each main tooth cusp has two smaller side cusps anteriorly, and two posteriorly, which have less developed anterior and posterior ridges, and lack the medial ridge (in the holotype and V7217.2).
Remarks: The new dentigerous jaw bones are in general shape similar to those of *Xylacanthus grandis* Ørvig from the Lower Devonian of Spitsbergen (Ørvig, 1967), but can be distinguished by the shape of the main tooth cusps in transverse section, and the presence of three stout dentine ridges on the main tooth cusps, and of two small tooth cusps attached posteriorly. They also differ slightly from *Persacanthus* (Janvier, 1977), but are clearly referable to the Ischnacanthida, the only acanthodians possessing such dentigerous jaw bones (Moy-Thomas and Miles, 1971; Denison, 1976, 1978).

genus indet.
Figs 6-8

Material: V7218.1,3,6 and 8, four isolated scales, and V7218.4 and 7, two longitudinal sections.

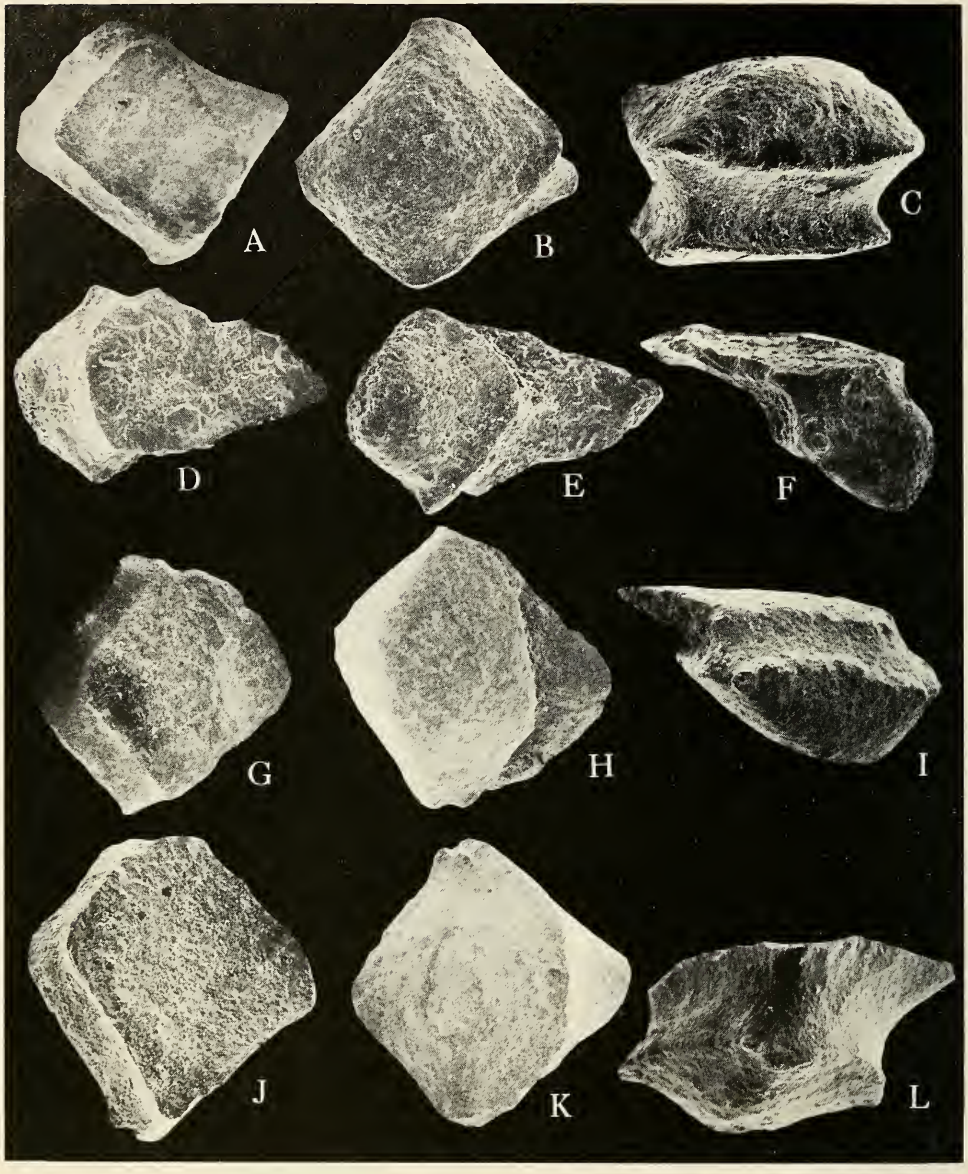


Fig. 6. Ischnacanthidae gen. indet. V7218, body scales. **A-C**, No. 6 (**A**, × 36; **B**, × 38; **C**, × 48). **D-F**, No. 3 (× 67). **G-I**, No. 1 (× 34). **J-L**, No. 8 (× 42). **A**, **D**, **G**, and **J**, crown views: **B**, **E**, **H**, and **K**, basal views; **C**, **F**, **I**, and **L**, lateral views.

Locality and Horizon: As for V7215.

Description: Of the many isolated scales at my disposal from the Xitun member, most are acanthodian scales of which the type exemplified by V7218 is the most common.

These scales have a more or less rhomboidal-shaped crown which is flat and smooth. The length of the crown may equal its breadth or be somewhat longer. The tumid scale base is longer than broad. The scale neck is clearly constricted. The an-

TABLE 3

Ischnacanthid indet. Dimensions of scales (in mm)

V 7218	Length of crown	Breadth of crown	Length of base	Breadth of base	Depth of scale
1	1.20	1.20	1.00	1.80	0.50
3	0.60	0.30	0.30	0.40	0.30
6	0.90	0.80	0.95	0.95	0.60
8	1.10	1.10	0.80	1.00	0.50

terior edge of the base is more advanced than that of the crown, but the posterior edge of the crown extends backwards past the edge of the base. Scale dimensions are given in Table 3.

The scales are made up of concentric layers of dentinous tissue in the crown, and of concentric layers of bone tissue in the scale base. The thick base of acellular bone lacks a pulp cavity. This structure is clearly of the acanthodian type.

Remarks. The scales described here are similar to *Ischnacanthus* in their flat and smooth scale crowns, and also resemble scales of *Acanthodes*. However, they are possibly not congeneric with either form, and may be referable to *Youngacanthus* gen. nov.

Subclass CHONDRICHTHYES

Genus *GUALEPIS* nov.

Diagnosis: Scales of varying size, with crowns more or less triangular in shape, and ornamented either with anterior stout ridges and corresponding deep furrows, or with a series of concentric minor ribs and carrying a dentate posterior margin; constricted neck with a few pulp openings behind the neck; rhomboidal scale base funnel-shaped, flat, or convex in ventral view, and having a small pulp cavity.

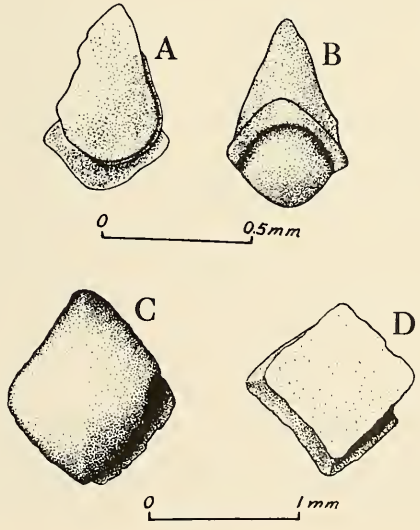


Fig. 7. Ischnacanthidae gen. indet. V7218, body scales. **A, B**, No. 3, crown view (**A**) and basal view (**B**), oriented with its posterior part upwards; **C, D**, No. 2, crown view (**D**) and basal view (**C**), oriented with its posterior part to the right.

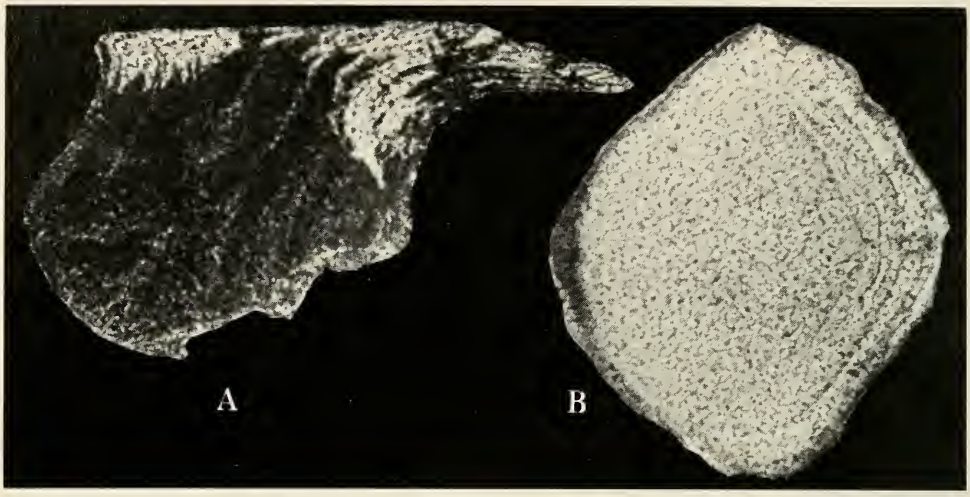


Fig. 8. Ischnacanthidae gen. indet. V7218. **A**, vertical longitudinal section of a body scale, No. 4 (× 134); **B**, crown horizontal section of a body scale, No. 7 (× 58.5).

Gualepis elegans sp. nov.
Figs 9-11

Derivation of name: After the late Professor M. R. Guo, previously Head of Academia Sinica; *lepis* (Gr.), a scale, and *elegans* (L.), fine.
Holotype: V7219.8, an old scale.
Paratype: V7219.3, a juvenile scale.
Other material: Many isolated scales of juvenile, adult, and old stages of growth.
Locality and Horizon: As for V7215.
Description: According to their stage of development and derivation from different areas of the body, the scales vary in size and shape. The juvenile scale has a thin crown and base, and a very clear neck. The crown is more or less triangular in shape. The length and width of the smallest scales are about the same, but with larger scales the width of the crown increases (Table 4). When the crown is broader than long it ranges in maximum rostrocaudal length from about 0.30 to 0.55 mm, and in maximum transverse breadth from about 0.40 to 0.80 mm. The crown has several anterior ridges and corresponding deep furrows which extend back to the middle of the crown surface. The number of ridges and furrows increases with the development of the scale. For example, there is only one furrow in specimen V7219.7, four ridges and three furrows in V7219.5, and six ridges and five furrows in the paratype. The crown carries a dentate posterior margin, in which the number of posterior denticles increases with scale growth. The paratype has about 19 denticles, but other scales may have a smooth posterior margin (e.g. V7219.5). The interior surface of the crown is smooth in all juvenile scales.

The juvenile scale has a clearly constricted neck, to which the ridges and furrows of the crown may extend (e.g. V7219.5). Visible posteriorly is a variable number of vascular canal openings between the crown and base (Ørvig, 1966). Specimen V7219.6, for example, shows 7 neck openings (*no,* Fig. 9**H, I**).

The rhomboidal base of the juvenile scale is more or less funnel-shaped in ventral view. The bases are broader than long and range in maximum rostrocaudal length from 0.20 to 0.30 mm, and in maximum transverse breadth from 0.30 to 0.60 mm.

TABLE 4

Gualepis elegans *gen. et sp. nov. Dimensions of scales (in mm)*

V 7219	Length of crown	Breadth of crown	Length of base	Breadth of base	Depth of scale
3	0.55	0.80	0.30	0.60	0.25
5	0.40	0.70	0.30	0.60	0.30
2	0.30	0.40	0.20	0.30	0.25
6	0.50	0.70	0.30	0.45	0.20
4	0.40	0.60	0.25	0.40	0.25
7	0.30	0.40	0.30	0.40	0.30
1	0.60	0.85	0.50	0.70	0.40
8	0.70	1.10	0.30	0.80	0.40
10	0.70	0.90	0.45	0.90	0.20
9	0.50	0.60	0.30	0.50	0.20
11	1.10	1.40	0.60	1.10	0.30
12	0.80	1.00	0.40	0.80	0.40
13	0.50	0.90	0.40	0.60	0.15

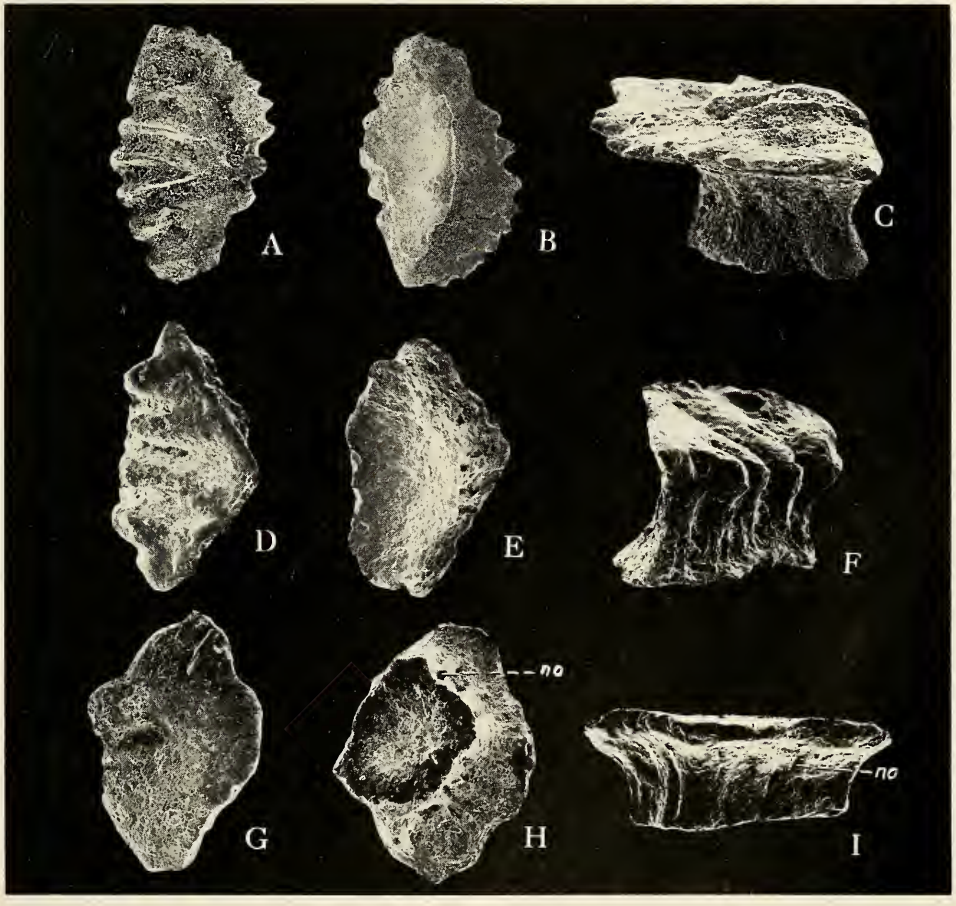
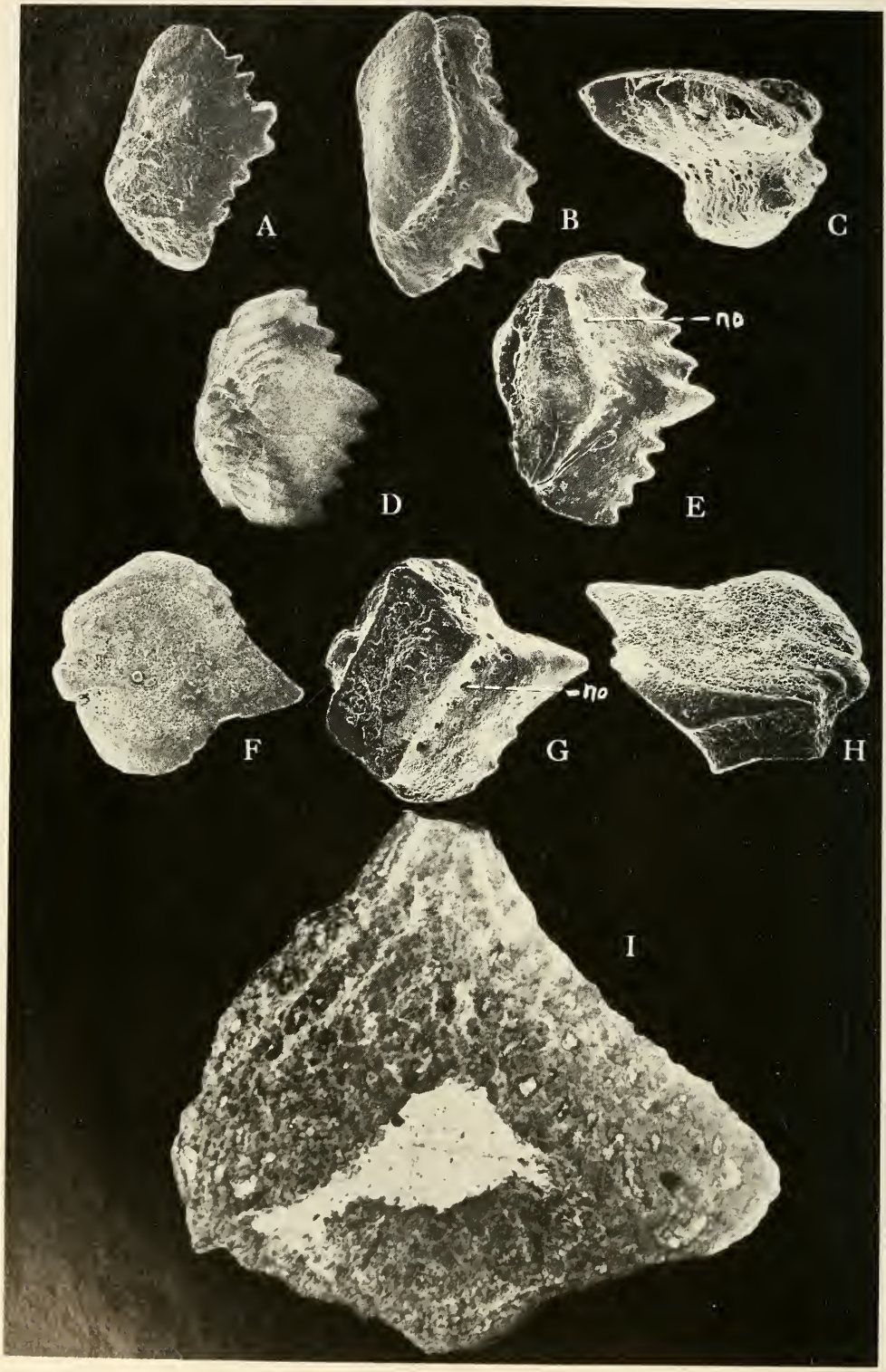


Fig. 9. Gualepis elegans gen. et sp. nov. V7219, juvenile scales. **A-C,** paratype (**A, B** × 51; **C,** × 80). **D-F,** No. 5 (× 55). **G-I,** No. 6 (× 68). **A, D,** and **G,** crown views; **B, E,** and **H,** basal views; **C,** oblique lateral view; **F,** oblique anterior view; **I,** posterior view. *no,* neck opening.


A
B
C
no
D
E
F
no
G
H
I

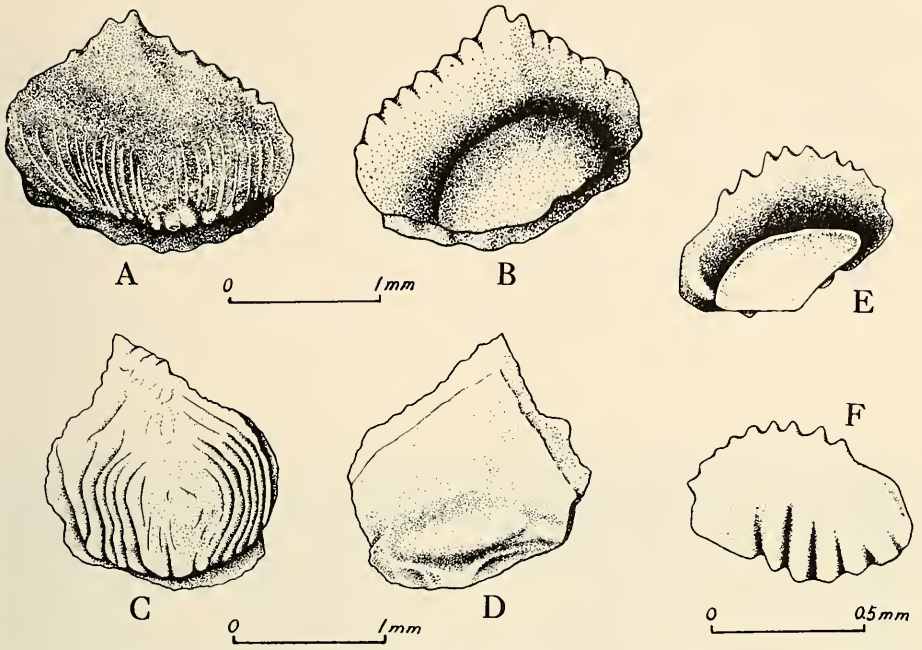


Fig. 11. Gualepis elegans gen. et sp. nov. V7219. **A, B**, an old scale, No. 1; **C, D**, an old scale, No. 4; **E, F**, paratype, a juvenile scale. **A, C,** and **F**, crown views; **B, D**, and **E**, basal views.

In length and breadth the scale crown equals the base in the smallest juvenile scales, but the scale crown is proportionately larger than the base in larger juvenile scales. The depth of juvenile scales is fairly constant (0.20 to 0.30 mm deep).

In mature and old scales the crown and base are thicker, and the crown is bigger than the base. The stout ridges of the juvenile stage decrease in number in adult and old scales (e.g. the holotype), or fuse to form a large anterior point as in specimen V7219.12. Some concentric minor ribs may develop on the exterior surface of the crown (e.g. V7219.12 has 7 ribs on each side). Posteriorly the crown can carry a few stout denticles. The maximum rostrocaudal length of the crown varies from 0.50 to 1.10 mm, and the maximum transverse breadth from 0.60 to 1.40 mm.

The rhomboidal scale base is again broader than long, with a maximum rostrocaudal length between 0.30 and 0.60 mm, and maximum transverse breadth between 0.50 and 1.10 mm. The base is flat or convex in basal view.

Remarks: These new scales recall in their general shape *Elegestolepis grossi* Kar.-Tal. from the Upper Silurian of Tuva (Karatajute-Talimaa, 1973), but they differ in having a more or less triangular crown, and carrying the characteristic ornamentation on the exterior surface of the crown with a few denticles along its posterior margin, and in possessing more neck openings. For these reasons a new genus and species has been erected. The affinities of such scales within the Chondrichthyes are at present uncertain.

Fig. 10. Gualepis elegans gen. et sp. nov. V7219. **A-C**, holotype, an old scale. **A**, crown view (× 38); **B**, basal view (× 41); **C**, lateral view (× 57.5). **D, E**, an old scale, No. 9 (**D**, × 38; **E**, × 43). **F-H**, an adult scale, No. 7 (**F**, × 62; **G**, × 67; **H**, × 80). **I**, crown horizontal section of an old scale, No. 2 (× 80).

TABLE 5

Changolepis tricuspidus *gen. et sp. nov. Dimensions of scales (in mm)*

V 7220	Length of crown	Breadth of crown	Length of base	Breadth of base	Depth of scale
1	0.70	0.80	0.50	0.70	0.45
2	0.70	0.80	0.60	0.70	0.30
3	0.80	0.90	0.80	0.85	0.50
4	0.50	0.60	0.35	0.50	0.30
5	0.70	0.80	0.50	0.70	0.20

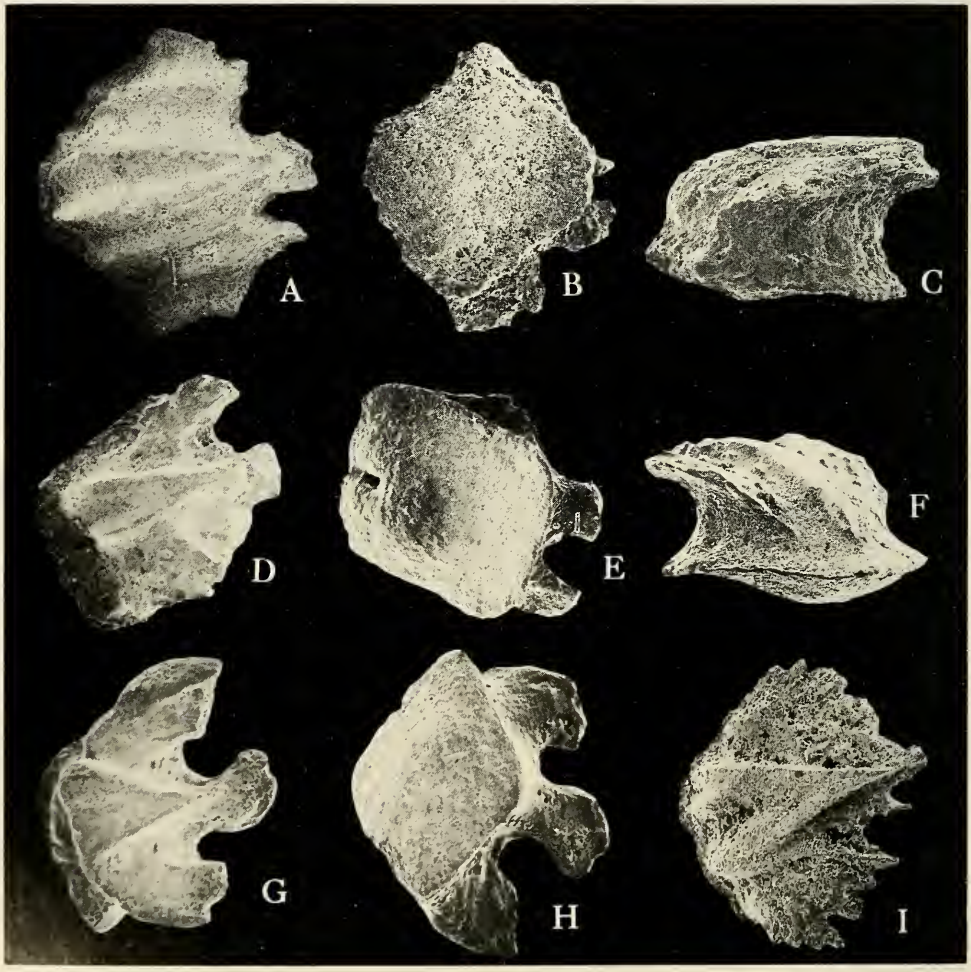


Fig. 12. Changolepis tricuspidus gen. et sp. nov. V7220. **A-C**, paratype (× 52); **D-F**, No. 8 (× 40); **G, H**, holotype (× 40); **I**, No. 9 (× 48). **A, D, G**, and **I**, crown views; **B, E**, and **H**, basal views; **C** and **F**, lateral views.

Genus *CHANGOLEPIS* nov.

Diagnosis: Scale having a more or less rhomboidal crown, with ornamentation on the exterior surface divided into three parts: a strongly convex central rib which forms a long main cusp posteriorly, and lower lateral ribs which have shorter posterior cusps; neck region well defined, with a few neck openings; rhomboidal scale base funnel-shaped, flat, or convex in basal view.

Changolepis tricuspidus sp. nov.

Fig. 12

Derivation of name: After the late Professor C. L. Chang, who first systematically studied fish fossils in China, and *tricuspidis* (L.), three pointed.

Holotype: V7220.1, an old scale.

Paratype: V7220.2, a juvenile scale.

Other material: Eight isolated scales at juvenile, adult, and old stages of growth.

Locality and Horizon: As for V7215.

Description: The specimens included here are isolated scales. They have a more or less rhomboidal crown which is slightly broader than long, and ranges in maximum rostrocaudal length from 0.50 to 0.80 mm, and in maximum transverse breadth from 0.60 to 0.90 mm (Table 5). The ornamentation on the exterior surface of the crown is divided into three parts: a strongly convex central rib forms a long main cusp posteriorly, and two lower lateral ribs have shorter posterior cusps. The neck is constricted, and posteriorly has a clear neck opening between the crown and base (e.g. specimen V7220.3). The rhomboidal base is broader than long, and varies in maximum rostrocaudal length from 0.35 to 0.80 mm, and in maximum transverse breadth from 0.50 to 0.85 mm. The shape of the base in basal view is variable in different scales; it is funnel-shaped in V7220.5, flat in V7220.4, convex anteriorly and flat posteriorly in V7220.2 and 3, and slightly convex in V7220.1.

Remarks: These scales are similar to the placoid scales described from the Middle Permian of Japan (Reif and Goto, 1979), but they differ greatly from the latter in many characters, in particular in the shape of the scale neck and base. They are therefore proposed as a new scale form, *Changolepis tricuspidus* gen. et sp. nov.

Genus indet.

Fig. 13

Material: Four isolated teeth, two complete (V7221.1 and 2), and two incomplete (V7221.3 and 4).

Fig. 13. Chondrichthyan? indet. V7221, an isolated tooth (× 60).

TABLE 6

Chondrichthyan? indet. Dimensions of teeth (in mm)

V 7221	Maximum breadth of tooth	Depth of main cusp	Breadth of base in main cusp	Depth of interior side cusps	Depth of exterior side cusps
1	0.60	0.50	0.22	0.30	0.20
2	0.68	0.65	0.35	0.40	0.14

Locality and Horizon: As for V7215.

Description: These four teeth vary in size (Table 6), but have the same shape, with a relatively small base and smooth, conical cusps. There is a high central cusp, and two pairs of low side-cusps of which the outer cusps are the smaller. The tooth consists of a dentine crown covered by a shiny, very hard, enamel-like substance. The base is usually broken, but a few openings of vascular canals can be observed. A few tubercles between the cusps and the base are arranged in two rows: smaller ones near the cusps, and larger near the base. Perhaps the connective tissue was attached to these tubercles.

Remarks: These specimens show some resemblance to teeth or denticles of elasmobranchs, for example the Carboniferous form *Symmorium* Cope. On the other hand they are not dissimilar to some figured teeth of climatiid acanthodians (e.g. Denison, 1979: fig. 13A). If the chondrichthyan affinities of these teeth are confirmed, they may prove to belong either to *Gualepis,* or to *Changolepis.*

Genus *PEILEPIS* nov.

Diagnosis: Scales with an elliptical crown, bifurcated posteriorly; surface of crown with three flutings and some minor ribbings; scale base flat and rhombic-shaped; scale neck well defined, with three small posterior neck openings; pulp cavity large and wide.

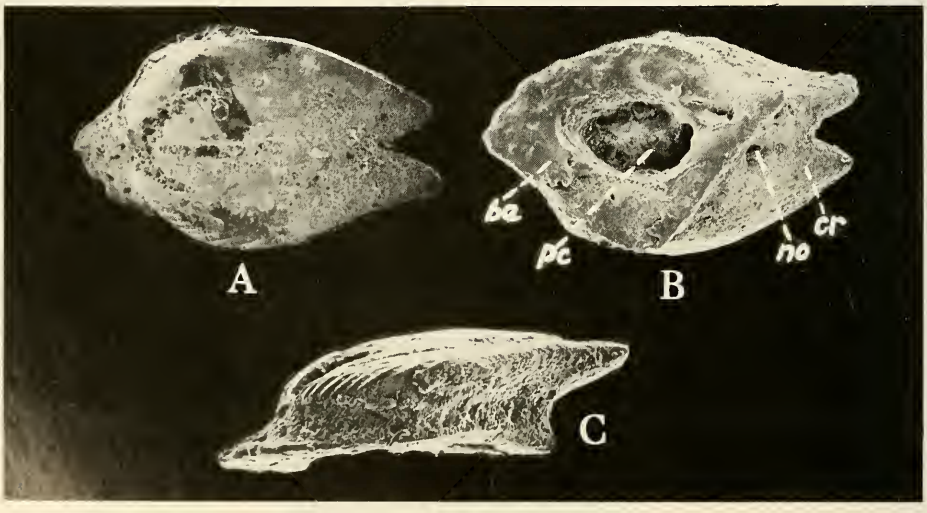


Fig. 14. Peilepis solida gen. et sp. nov. V7222, a body scale. **A**, crown view, **B**, basal view, and **C**, latero-crown view (⁄ 45). *ba,* base; *cr,* crown; *no,* neck opening; *pc,* pulp cavity.

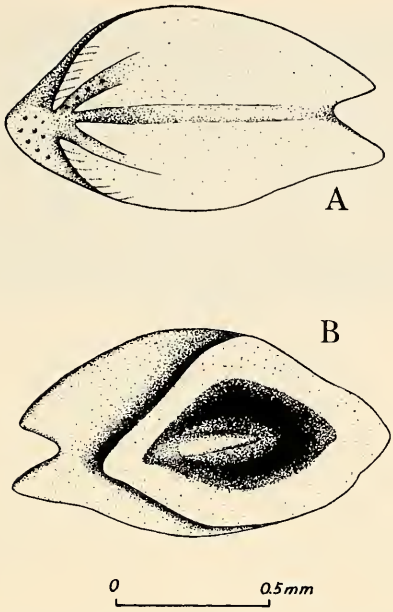


Fig. 15. Peilepis solida gen. et sp. nov. V7222. **A**, crown view; **B**, basal view.

Peilepis solida sp. nov.
Figs 14, 15

Derivation of name: After the late Professor Pei, and *solidum* (L.), dense.
Diagnosis: As for genus (only species).
Holotype: V7222, a body scale.
Locality and Horizon: As for V7215.
Description: This complete isolated scale is composed of a scale crown, base, and neck region. The crown is elliptical and flat, with a maximum rostrocaudal length of 1.1 mm, and maximum transverse breadth of 0.75 mm. There are three flutings on the anterior part of the crown surface. The middle one is longer than the two V-shaped lateral ones. There are also 14 fine parallel ribbings on the anterolateral margins. The posterior part of the crown is bifurcated and extends back over the base. The base is flat, and approximately rhombic in shape. Its maximum rostrocaudal length is 1.0 mm, and its maximum transverse breadth is 0.65 mm. The anterior part of the base extends in front of the crown. The base possesses a large, wide, elliptical pulp opening, 0.5 mm long and 0.3 mm wide. The scale neck is distinct, and carries posteriorly three small rounded foramina (*no,* Fig. 14**B**).
Remarks: Is is clear that this scale belongs to a chondrichthyan, but there is no previously described material resembling this scale. It differs from *Gualepis elegans* gen. et sp. nov. and the other kinds of chondrichthyan scales produced from the same layer in having an elliptical crown, bifurcated posteriorly, with a special ornamentation, and a large wide pulp cavity. A new scale genus and species has therefore been erected.

Genus *OHIOLEPIS* ? Wells 1944
Ohiolepis? xitunensis sp. nov.
Figs 16, 17

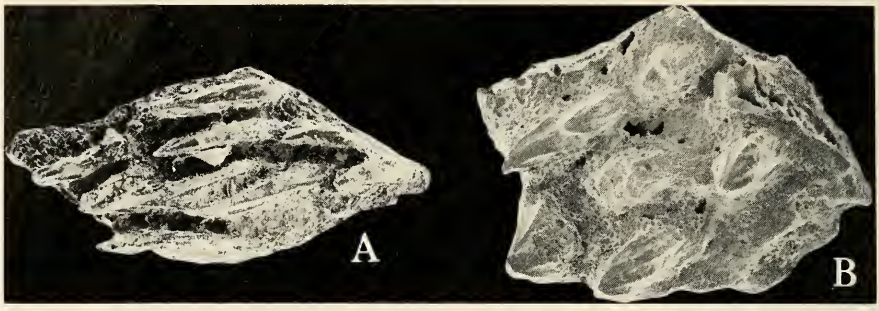


Fig. 16. Ohiolepis? xitunensis sp. nov. V7223. **A**, complete scale, crown view, No. 1 (× 30); **B**, incomplete scale, crown view (× 50).

Diagnosis: A complex scale of rhomboidal shape and consisting of denticles arranged in four rows, which slope backwards, with spaces between rows and between adjacent denticles; each cone-shaped denticle covered by a thin layer of dentinous tissue and carrying a few ribs; base of the scale flat, with a clear, central part in ventral view.
Holotype: V7233.1, a complete scale.
Other material: V7223.2, an incomplete scale.
Locality and Horizon: As for V7215.
Description: The holotype is a complete, highly specialized complex scale. It has a rhomboidal base, giving the scale its rhomboidal shape. Its maximum rostrocaudal length is 2 mm, and its maximum transverse breadth is 0.9 mm. The scale crown consists of nine denticles arranged in four rostrocaudal rows which slope backwards. The tips of the most posterior denticles project over the posterior margin of the scale. There are spaces between adjacent rows and adjacent denticles. Each cone-shaped denticle is covered by a thin dentinous layer which carries three to five longitudinal ribs at its surface. The base of the scale is flat, and possesses in ventral view a clear central part which perhaps contains all pulp openings of the denticles.
Remarks: These scales show some resemblance to those of *Ohiolepis* (e.g. Gross, 1973: pl. 31), to which this new species is provisionally referred for the purposes of description. It is certainly not conspecific with *Ohiolepis newberryi* Wells from the Middle Devonian of Ohio, USA, which differs in the shape of the denticles, and the shape and structure of the base. On the other hand the rhomboidal shape, and the pores opening to the surface between the denticles, are somewhat reminiscent of early teleostome scales (e.g. Gross, 1969). More material is required to permit a histological examination of this scale type, so that its proper affinity can be established. For the present it is tentatively included with the other chondrichthyan scales from the Xitun member.

Discussion

Many areas of the world were apparently not part of the main tectonic blocks of Laurentia, Angaraland, and Gondwanaland, yet these may have played a critical role in providing terrestrial connections between the major tectonic blocks (Turner and Tarling, 1982). Such an example is the South Chinese block. The new thelodont, acanthodian and chondrichthyan remains from the Lower Devonian of southwest China should provide some evidence of this.

Turinia asiatica sp. nov. has been compared with *Turinia polita*, Kar.-Tal. from the Lower Devonian of Lithuania, Volynia, and Podolia, USSR, and *Thelodus trilobata*

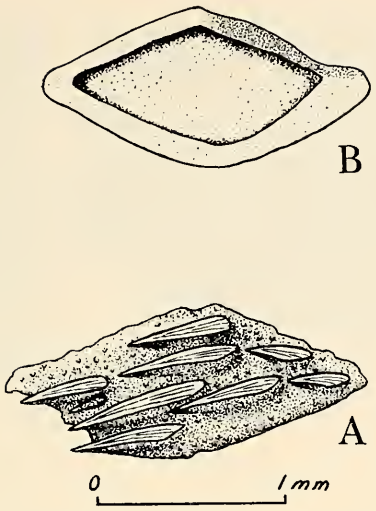


Fig. 17. Ohiolepis? xitunensis sp. nov. V7223, No. 1. **A**, crown view; **B**, basal view.

from the Ludlow and lower Downtonian of Europe. *Youngacanthus gracilis* gen. et sp. nov. resembles *Xylacanthus grandis* Ørvig from the Lower Devonian of Spitsbergen, and *Gualepis elegans* gen. et sp. nov. is similar to *Elegestolepis grossi* Kar.-Tal. from the Upper Silurian of Tuva, USSR.

In addition, the crossopterygian *Youngolepis praecursor* Zhang and Yu (1981) resembles *Powichthys* Jessen from the Lower Devonian of the Canadian Arctic, and *Szelepis yunnanensis* Liu (1979) is similar to *Kujdanowiaspis* from the Lower Devonian of Podolia.

In such circumstances there is reason to believe that the vertebrate fauna in the Xitun Member shows affinity to that of Baltica and North America in the Early Devonian. Thus, the relation between the South China block and Baltica and North America may have been closer in the Early Devonian than that between it and the other main tectonic blocks. However, it is difficult to ascribe the dispersal of thelodonts across the South China and Baltica blocks during the Early Devonian to direct land connections, or to the result of temporary land-bridge connections.

During the study of thelodont scales, the author has noted the similarity between some European Silurian thelodont scales and the ornamentation of the cephalic shield in the eugaleaspid agnathan *Hanyangaspis* Pan and Wang (1978) from the Middle Silurian of Hubei Province, China (see Pan, 1984). Each ornament tubercle of the cephalic shield in *Hanyangaspis* looks like a snowflake. It is subdivided by deep furrows forming numerous fine ridges, which converge towards the centre of the tubercle and tend to bifurcate at its outer margin (Fig. 18). The ornament surface is slightly convex or flat.

It is of interest that each of these tubercles is closely comparable to the crown of an individual scale in *Thelodus sculptilis* Gross (1967) or *T. admirabilis* Marss (1982) from the late Ludlovian to Early Devonian in Baltica and Western Russia, and to the ornament of *Porophoraspis crenulata* Ritchie and Tomlinson (1977) from the Middle Ordovician of Australia. This could indicate that the cephalic shield of forms like *Hanyangaspis* or *Latirostraspis* Wang *et al.* (1980) from the Middle Silurian of Anhui Province, China, was derived from the coalescence of many thelodont scale-like

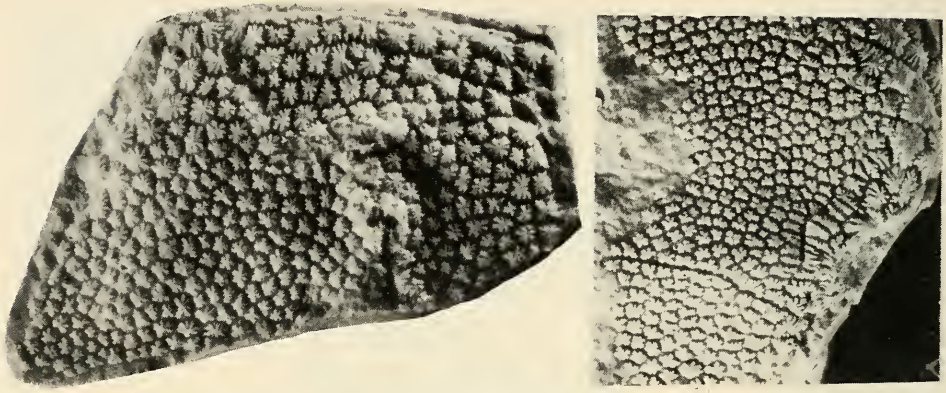


Fig. 18. Two moulds of the ornament of the cephalic shield in *Hanyangaspis* Pan and Wang (× 2).

tesserae. This might be supposed to have occurred with the crowns of the tesserae remaining free from each other, while the upper part of each base fused together, but with the limits of the lower part of each base still distinguishable on the inner surface of the shield. The mode of formation of the cephalic shield in *Hanyangaspis* may thus have been similar to that of the heterostracans. If this was the case, it is possible that there may have been some primitive thelodont-like agnathans in China before the Middle Silurian (Ordovician or Cambrian), from which *Hanyangaspis, Latirostraspis,* and the advanced thelodonts could have developed. This would assume that the cephalic shield of eugaleaspids evolved independently of the corresponding structure in other agnathan groups.

Turning now to the occurrence of acanthodian dentigerous jaw bones and scales in the Xitun Member, these are the first certain records of Early Devonian acanthodian remains from Yunnan Province. Previously in the Early Devonian of Yunnan two acanthodian species have been described: *Asiacanthus multituberculatus* T. S. Liu (1948) and *Yunnanacanthus cuifengshanensis* S. F. Liu (1973). However, Denison (1978) suggested that *Asiacanthus* and *Yunnanacanthus* may not be acanthodian remains, but probably spinal plates of Placodermi indet. After restudy and judging by new material, S. F. Liu (1982) has referred *Asiacanthus multituberculatus* and *Yunnanacanthus cuifengshanensis* to the arthrodires.

It is interesting that in South China there is another acanthodian assemblage consisting of more or less complete fin spines, from the Silurian in the region of the middle and lower reaches of the Yangtze River. The systematic position of these acanthodian genera is not clear, but it seems that they probably also belong to the Climatiida and Ischnacanthida (but are not congeneric or conspecific with those from the Xitun Member). This is based on my new finds of ischnacanthid tooth whorls and some typical acanthodian fin spines from the same horizon in this region. These new tooth whorls and fin spines will be described in another paper.

Regarding the discovery in the Xitun microvertebrate assemblage of many chondrichthyan scales of varying size and shape, it is noteworthy that these are much more abundant in the argillaceous limestones of the Xitun Member than in the siltstones. This is the first record of chondrichthyan fossils from the Devonian deposits of China. They not only enlarge the Lower Devonian vertebrate assemblage known from the Xitun Member, but give some new evidence for determining the depositional environment of the Xitun Member.

Previously, some authors (e.g. Liu and Wang, 1973) considered that the Xitun Member was predominantly a continental deposit, on the basis of its supposed freshwater fishes (e.g. *Polybranchiaspis, Yunnanolepis,* etc.). But other authors (e.g. Li and Cai, 1978) regard the Xitun Member as a marginal marine or brackish deposit (perhaps near a river mouth), on the evidence of fossil algae *(Uncatoella verticillata, Discinella cuifengshanensis),* pelecypods, and brachiopods (*Lingula* sp.).

Most Palaeozoic chondrichthyans occur in marine or paralic deposits, and may be assumed to have been marine. Only two elasmobranch groups make an exception to this; members of the ctenacanth and xenacanth sharks were either freshwater or euryhaline (Zangerl, 1981). However, these are typically Late Devonian or younger forms, and there is no clear indication that the scales described here belong to either of these groups. The new scales support the view that the Xitun Member, which is the richest layer both in diversity and abundance of Agnatha and fish fossils from the Cuifengshan Formation, was probably a marginal marine deposit, as indicated by its chondrichthyan, invertebrate, and algal fossils.

To conclude, the vertebrate assemblage from the Xitun Member of the Cuifengshan Formation (Qujing district of Yunnan), including the new forms described above, may be listed as follows:

eugaleaspids:	*Polybranchiaspis liaojiaoshanensis* Liu, 1965
	Eugaleaspis (Galeaspis) changi Liu, 1965
	Nanpanaspis microculus Liu, 1965
	Laxaspis qujingensis Liu, 1965
thelodontids:	*Turinia asiatica* sp. nov.
acanthodians:	*Youngacanthus gracilis* gen. et sp. nov.
	Ischnacanthidae gen. indet.
	Nostolepis sp. indet.
crossopterygians:	*Youngolepis praecursor* Zhang and Yu, 1981
dipnoans:	*Diabolichthys* Zhang and Yu, 1984
arthrodires:	*Szelepis yunnanensis* Liu, 1979
antiarchs:	*Yunnanolepis chii* Liu, 1963
	Y. parvus Zhang Guorui, 1978
	Phymolepis cuifengshanensis Zhang Guorui, 1978
	Qujinolepis gracilis Zhang Guorui, 1978
	Zhanjilepis aspratilis Zhang Guorui, 1978
chondrichthyans:	*Gualepis elegans* gen. et sp. nov.
	Changolepis tricuspidus gen. et sp. nov.
	Peilepis solida gen. et sp. nov.
	Ohiolepis ? xitunensis sp. nov.

Acknowledgements

It is a pleasure to record my thanks to the Australian Academy of Science, the Australian Museum and the Association of Australasian Palaeontologists, who gave a favourable opportunity of presenting my work at the Symposium on the Evolution and Biogeography of Early Vertebrates.

I thank Profs K. S. W. Campbell, D. L. Dineley and H. P. Schultze, Drs A. Ritchie, D. Goujet, Ph. Janvier, G. C. Young, and M. M. Zhang, who contributed valued criticism and stimulating discussions to an earlier draft of this paper. I also thank Drs V. N. Karatajute-Talimaa, S. Turner and W. E. Reif, who kindly provided their works; Dr G. C. Young for improving the English of the manuscript, and giving some Australian thelodont scales, Prof. X. Y. Li, for reading the paper in manuscript,

Mr Y. Hu for SEM photography, Mr Z. Du and W. D. Gui for optical photography, Mrs J. S. Dai for text figures and retouching photographs, and Mrs S. W. Wang and Mr Z. Y. Liu for typing the manuscript.

References

Blieck, A., and Goujet, D., 1978. — A propos de nouveau matérial de Thelodontes (Vertébrés, Agnathes) d'Iran et de Thailande: aperçu sur la repartition géographique et stratigraphique des Agnathes des 'régions gondwaniennes' au Paléozoique moyen. *Ann. Soc. Geol. Nord,* Lille 97: 363-373.

Berg, L. S., 1940. — Classification of fishes, both Recent and fossil. *Trav. Inst. Zool. Acad. Sci. URSS* 5: 85-517.

Denison, R. H., 1976. — Note on the dentigerous jaw bones of Acanthodii. *N. Jb. Geol. Palāont., Monatsh.* 1976: 395-399.

———, 1978. — Placodermi. *Handbook of Paleoichthyology,* vol. 2, H.-P. Schultze (ed.). Stuttgart: Gustav Fischer Verlag.

———, 1979. — Acanthodii. *Handbook of Paleoichthyology,* vol. 5, H.-P. Schultze, (ed.). Stuttgart: Gustav Fischer Verlag.

Gross, W., 1940. — Acanthodier und Placodermen aus *Heterostius*-Schichten Estlands und Lettlands. *Ann. Soc. Reb. Natur. Invest. Univ. Tartuensis const.* 46: 1-89.

———, 1947. — Die Agnathen und Acanthodier des obersilurischen Beyrichien Kalks. *Palaeontographica* A96: 91-161.

———, 1957. — Mundzahne und Hautzahne der Acanthodier und Arthrodiren. *Palaeontographica* A109: 1-40.

———, 1967. — Über Thelodontier-Schappen. *Palaeontographica* A127: 1-167.

———, 1969. — *Lophosteus superbus* Pander, ein Teleostome aus dem Silur Oesels. *Lethaia* 2: 15-47.

———, 1971. — Downtonische und dittonische Acanthodier — Reste des Ostseegebietes. *Palaeontographica* A136: 1-82.

———, 1973. — Kleinschuppen, Flossenstacheln und Zähne von Fischen aus europäischen und nordamerikanischen Bonebeds des Devons. *Palaeontographica* A142: 51-155.

Hoppe, K. H., 1931. — Die Coelolepiden und Acanthodier des Obersilurs der Insel Ösel. *Palaeontographica* A76: 35-94.

Janvier, P., 1977. — Les poissons devoniens de l'Iran central et de l'Afghanistan. *Mem. Soc. Geol. France* 8: 277-289.

Karatajute-Talimaa, V. N., 1973. — *Elegestolepis grossi* gen. et sp. nov. ein neuer Typ des Placoidschuppe aus dem Oberen Silur der Tuwa. Gross-Festschrift, *Palaeontographica* A143: 35-50.

————————, 1978. — *Silurian and Devonian Thelodonts of USSR and Spitsbergen.* Mosklas, Vilnius.

Li, X. X., and Cai, C. Y., 1978. — A type-section of Lower Devonian strata in southwest China with brief notes on the succession and correlation of its plant assemblages. *Acta Geologica Sinica* 1: 1-14.

Liu,S. F., 1973. — Some new Acanthodian fossil materials from the Devonian of South China. *Vertebr. PalAsiat.* 11: 144-147.

———, 1982. — Preliminary note on the Arthrodira from Guangxi, China. *Vertebr. PalAsiat.* 22: 106-114.

Liu, T. S., 1948. — Note on the first occurrence of Acanthodians from China. *Palae. Nov. China* 4.

Liu, Y. H., 1965. — New Devonian agnathans of Yunnan. *Vertebr. PalAsiat.* 9: 125-134.

———, 1975. — Lower Devonian agnathans of Yunnan and Sichuan. *Vertebr. PalAsiat.* 13: 215-223.

———, 1979. — On the arctolepid Arthrodira from Lower Devonian of Yunnan. *Vertebr. PalAsiat.* 17: 23-33.

———, and Wang, J. Q., 1973. — Some problems on Devonian stratigraphy of eastern Yunnan. *Vertebr. PalAsiat.* 11: 1-17.

Märss, T., 1982. — *Thelodus admirabilis* n. sp. (Agnatha) from the upper Silurian of the East Baltic. *Eesti. NSV Tead. Akad. Toim. Keem.-Geol.* 31: 112-115.

Moy-Thomas, J. A., and Miles, R. S., 1971. — *Palaeozoic fishes.* 2nd ed. London: Chapman and Hall.

Obruchev, D. V., 1964. — Class Placodermi. *In* I. A. Orlov, (ed.) *Fundamentals of Paleontology,* 11. *Agnatha, Pisces* (D. V. Obruchev, ed.): 118-171, Nauka: Moscow (in Russian).

Ørvig, T., 1966. — Histological studies of ostracoderms, placoderms and fossil elasmobranchs. 2. On the dermal skeleton of two late Palaeozoic elasmorebranchs. *Ark. Zool.* 19: 1-39.

———, 1967. — Some new acanthodian material from the Lower Devonian of Europe. *J. Linn. Soc. London (Zool.)* 47: 131-153.

Pan, J., 1984. — The phylogenetic position of the Eugaleaspida in China. *Proc. Linn. Soc. N.S.W.* 107: 309-319.

——, and WANG, S. T., 1978. — Devonian Agnatha and Pisces of South China. In: *Symposium on the Devonian system of South China.* 1974: 298-333, Peking: Geological Press.

REIF, W. E., and GOTO, M., 1979. — Placoid scales from the Permian of Japan. *N. Jb. Geol. Paläont. Monatsh.* 1979(4): 201-207.

RITCHIE, A., and GILBERT-TOMLINSON, J., 1977. — First Ordovician vertebrates from the Southern Hemisphere. *Alcheringa* 1: 351-368.

TURNER, S., 1976. — Thelodonti (Agnatha), *Fossilium catalogus Pars 122. Animalia*: 1-35.

——, and TARLING, D. H., 1982. — Thelodont and other Agnathan distribution as tests of lower Palaeozoic continental Reconstructions. *Palaeogr. Palaeocl. Palaeoecol.* 39: 295-311.

WANG, S. T., XIA, S., CHEN, L., and DU, S., 1980. — On the discovery of Silurian Agnathans and Pisces from Chaoxian county, Anhui Province and its stratigraphical significance. *Bull. Chinese Acad. Geol. Sci.* 1: 103-112.

YOUNG, G. C., 1981. — Biogeography of Devonian vertebrates. *Alcheringa* 5: 225-243.

——, 1982. — Devonian sharks from south-eastern Australia and Antarctica. *Palaeontol.* 25: 817-843.

ZANGERL, R., 1981. — *Chondrichthyes* I. Paleozoic Elasmobranchii. *Handbook of Paleoichthyology,* vol. 3A. H.-P. SCHULTZE, (ed.). Stuttgart: Gustav Fischer Verlag.

ZHANG, G. R., 1978. — The antiarchs from the Early Devonian of Yunnan. *Vertebr. PalAsiat.* 16: 147-186.

ZHANG, M. M., and YU, X., 1981. — A new crossopterygian, *Youngolepis praecursor* gen. et sp. nov., from the Lower Devonian of E. Yunnan, China. *Scient. Sinica* 24: 89-97.

——, and ——, 1984. — Structure and phylogenetic significance of *Diabolichthys speratus* gen. et sp. nov., a new dipnoan-like form from the Lower Devonian of eastern Yunnan, China. *Proc. Linn. Soc. N.S.W.* 107: 171-184.